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OF
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BY C. O. WHITMAN. ✓

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THE SEGMENTAL SENSE-ORGANS OF THE LEECH.

BY DR. C. O. WHITMAN.

THE only sense-organs hitherto known in the medicinal leech are the five pairs of eyes and the so-called "goblet-shaped" organs located in the edge of the lip (cephalic lobe). A number of writers have noticed and described some small spots occurring on every fifth ring of the body; and one author has suggested that they may have a respiratory function. But no one, so far as the published accounts inform us, has intimated that they represented sense-organs, or suspected that they were the serial homologues of the eyes themselves. These spots, when examined closely with a low magnifying power, will be found to be slight elevations with rounded summits, and for this reason and because they are regularly disposed on the first ring of each segment (somite) they may be called segmental papillæ, a name which does not prejudge the question of their function. In our large pond leech (*Macrobdella*) these papillæ are comparatively small; and the same may be said of the medicinal leeches of Europe and Japan, and their nearest allies, *Hæmopsis* and *Aulostoma*. In some of the Asiatic medicinal leeches, for example, those of Saigon, Singapore (*H. maculosa*), Java (*H. javanica*) and Ceylon (*H. multistriata*), they are much larger and have an oval form with a median ridge or crest. In the land leeches they are very conspicuous, having the form of small cones with rounded summits.

In all the ten-eyed leeches of Japan, including both the land and fresh-water forms, twelve of these papillæ are found on the first ring of each complete somite, six on the dorsal and six on the ventral side. In most of the medicinal leeches, however, as well as in *Hæmopsis*, *Aulostoma*, *Macrobdella*, &c, there are eight on the dorsal side and six on the ventral.

A careful study of the *arrangement* of these papillæ in a large number of species, and of their histological structure, has brought out in a most conclusive manner their *serial homology with the eyes*; and has led, indirectly, to the recognition of some important points in regard to the metameric composition of the body of the leech. The accompanying diagram will enable me to be brief. The eyes are represented by five pairs of large black dots, the segmental papillæ by smaller dots. The numerals on the

left give the number of somites, those on the right the number of the first ring of each somite. The position of the seventeen pairs of nephridial pores is shown by short dashes (*1st p-17th p*). With the exception of the genital and nephridial pores, the diagram shows only what belongs to the dorsal side. It will be seen that there are twenty-six *transverse* rows of papillæ—one for each somite; and that, owing to their uniform and symmetrical arrangement, they form also eight *longitudinal* rows. We have *two median* rows (*m*) formed of twenty-five successive pairs; *four lateral* rows, an *inner* (*il*) and an *outer* (*ol*) on each side of the median line; and *two marginal* rows (*mg*). The first two eyes hold the position of a pair of median papillæ, while the remaining eyes replace as many *inner lateral* papillæ. About this correspondence in position there is not, in my opinion, any room for doubt. In the diagram the outer lateral and the marginal papillæ are to be seen as far forward as the first eye-bearing ring, the marginal ones alone being absent on this ring; but in most species of *Hirudo* both of these rows of papillæ are very indistinct or entirely absent on the first three eye-bearing rings. They are present in *Aulostoma*, and are very distinct in the large medicinal leeches of Saigon, Singapore, Java and Ceylon.

The median rows of papillæ, if their position is not misleading, must be regarded as the metameric equivalents of the *first* pair of eyes; the inner lateral rows hold the same relation to the second, third, fourth and fifth pairs of eyes. There is a possibility that the first pair of eyes are derivatives of the inner lateral papillæ, the median papillæ of this ring having been lost and the eyes brought nearer together so as to stand in line with the median papillæ of the following somites. However, as all the papillæ have the same structure, there is no objection on this score to the opinion that the eyes are derived from both the median and the inner lateral papillæ.

The structure of the papillæ confirms the homology above indicated, if one feature alone be excepted. The eye of the leech, as is well known, is a cylindrical mass of cells, three or four times as long as wide. The central or axial portion is made up of peculiar large glassy cells, in general appearance entirely unlike the other cells of the body. What the peculiarities of these cells are cannot well be explained without illustrative drawings; but for present purposes it will be sufficient to say that each of

these cells has a vacuole-like space occupying a central position which is probably filled with some kind of fluid. Whatever this fluid may be, it is not colored by any of the dyes in common use. The protoplasm of these cells forms a thick peripheral envelope with a rounded thickening on one side which projects into the vacuolar space. The very small nucleus is usually located near the base of this internal protuberance. This axial portion consisting of clear cells is enveloped by a thick layer of pigment on all sides except the external end. The epidermal cap covering these cells is convex, and entirely free from pigment, forming thus a window-like opening into the black pigment-cup which holds the large transparent cells. An optic nerve enters the eye near its deeper end, and runs along the axis for a larger portion of its length. It is probable that branches of the nerve connect with the clear cells, but precisely how has not been ascertained.

In sections of the segmental papillæ we find all the elements of the eye except the pigment. There is a branch of the lateral nerves that runs to each; and from four to six or more of those peculiar large glassy cells are found a little below the epidermal cap, which is convex and free from pigment.

The absence of a pigment-cup holding the glassy cells makes it doubtful whether the papillæ can be regarded as light-perceiving organs, but it does not, to my mind, weaken the evidence of their serial homology with the eyes. It is generally found that the posterior eyes, especially the fifth pair, are smaller than those preceding them; and I have noticed cases in which only a mere trace of pigment could be seen in one or both of the last pair of eyes. While it appears doubtful what the function of the papillæ is; still, the presence of large cells precisely like those in the eye, situated just below a window-like opening in the surface pigment, and their obvious serial equivalence with the eyes, makes it not improbable that they represent incipient organs of vision.

Although the evidence appears to me conclusive that the eyes and the segmental papillæ were, originally, morphological as well as physiological equivalents, it does not of course follow necessarily that both now have the same functional significance. The original papillæ may have represented sense organs of a more or less indifferent order, among which, in the course of the historical development of the leech, a division of labor was introduced; a few at the anterior extremity becoming specialized as organs of

vision, the rest either remaining in their early indifferent condition, or becoming specialized in some other direction.

In order to get a clearer and fuller idea of the fact that the eyes are metameric organs representing merely structurally improved forms of the segmental papillæ, let us look more closely at the rings and the somites composing the body. As a glance at the diagram will show, there are in all 102 rings between the first pair of eyes and the posterior sucker; the last two or three are more or less imperfect. The papillate rings show us precisely how many somites there are. Of the *twenty-six* somites, *sixteen* (7-22 inclusive) have each five rings, while the remaining ten have from one to three rings. Of these abbreviated somites *six* form the anterior and *four* the posterior end. We notice that the abbreviation is greatest at the extreme ends, from which it is plain that it began at these points and progressed towards the center of the body. The first two somites have each a single ring, the third is represented by two rings, and the fourth, fifth and sixth each by three rings. The first six somites then include only thirteen rings, less than half the number contained in six complete somites, such as are seen in the middle region of the body. The twenty-third somite embraces three rings, and the twenty-fourth, twenty-fifth and twenty-sixth each two rings. The last four somites contain only nine rings. The abbreviation not only extends to a larger number of somites at the anterior end than at the posterior, but it has been carried farther in the individual somites, at least in the first and second. At both ends the papillate rings have been preserved, while the less important non-papillate rings have been in part or wholly suppressed. The suppression of rings takes place by consolidation, two successive rings gradually coalescing. The papillate ring may coalesce either with the preceding or the following ring. In the medicinal leech the fifth ring, bearing the fourth pair of eyes, is now in process of uniting with the sixth; while the eighth is absorbing the seventh. The evidence that these two rings are being swallowed up is seen first of all in the rings themselves, and secondly, in the different conditions which they exhibit in different species and genera. In *Hirudo* and several allied genera the sixth and seventh rings are comparatively narrow, and the grooves separating them from the fifth and eighth rings are entirely obliterated on the ventral side, so that here the four rings appear as two. On

the dorsal side they are still distinct, but not so deeply marked off from the fifth and eighth rings as from each other. The same process of consolidation is seen in *Hæmopsis*, *Aulostoma* and *Hæmadipsa*, but in different stages. In *Macrobdella* all four rings are distinct on both sides, but the consolidation has already begun, as the grooves separating the fifth from the sixth, and the seventh from the eighth, are not so deep as the groove between the sixth and seventh, or that between any two of the succeeding rings.

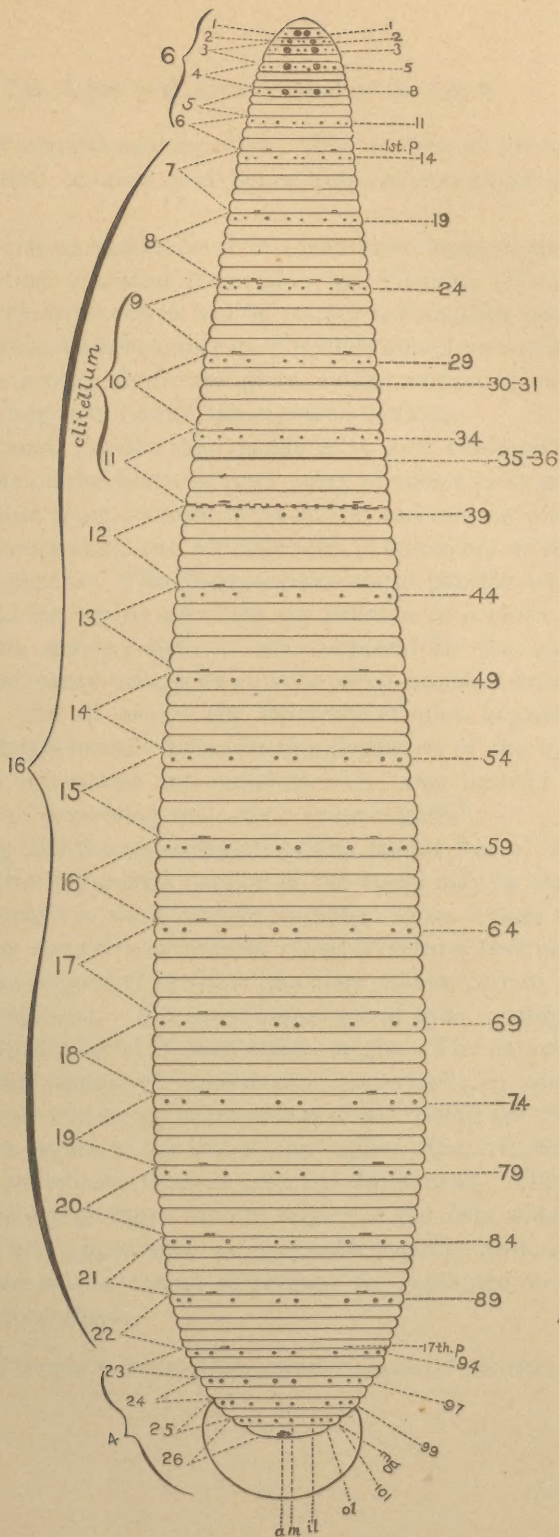
If the abbreviation is centripetal, we should expect the fourth ring to disappear before the sixth and seventh. This course of events has already been completed in the land leeches, in none of which is there a ring intervening between the third and fourth pairs of eyes.

Two non-papillate rings may also unite with each other; an instance is seen in the twenty-third somite of *Macrobdella*, where the second and third rings are well nigh consolidated.

The syncopation of rings has been carried farther in the acetabulum than in either of the posterior somites. In some species the segmental papillæ are quite distinct on the disk, and in these their arrangement shows that papillate rings alone have been preserved in this region.

The sacrifice of rings has been greatest in those parts that have been compelled to do the most work, namely, the two extremities. In the anterior somite the papillate rings have been preserved and functionally improved in proportion to the number of the less important non-papillate rings eliminated. In the posterior disk the loss of rings is not correlated with an improvement of the sense-organs, but with an increased development of muscles. The habits of the land leech have favored the development of a still greater muscular power in the disk, and this has been attended with a loss of five rings, leaving only four rings in its four terminal somites to offset nine rings on the aquatic leech.

If the historical development of the leech has been a progressive course of abbreviation such as we have described, it is evident that an ancestral form must have existed in which the somites were more nearly alike from end to end. The embryonic development confirms this view, for in its earlier phases the somites form a chain of very nearly equal parts. It is somewhat later that a few (7-8) of the posterior somites become constricted off and



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consolidated into the sucking disk. The somites at the anterior end are the first to arise and hence the first to exhibit specialization.

Among existing species three in Japan have departed less from the hypothetical ancestral form than has *Hirudo*. They agree with the medicinal leech in having twenty-six somites, but differ from it in having eighteen instead of sixteen complete somites. In one of these species there are plain evidences that abbreviation has already begun in one of the eighteen somites.

The segmental papillæ then enable us to give a tolerably complete analysis of the body, to read some chapters in its past history, to predict some portions of its future, and to draw a few safe conclusions respecting the phylogenetic relationship of different species and genera. The discovery that these papillæ are sense-organs might lead us to speculate on affinities of a more distant and uncertain nature; such as are supposed by the writer, in common with many others, to exist between annelid worms and vertebrates. At all events the existence of such organs in the leech furnishes a broader basis for the discussion of the question whether the vertebrates and annelids have been derived from a common form possessing metameric sense-organs.¹

Assuming that the sense-organs of the lateral line of the vertebrate and the segmental papillæ of the leech may be traced to a common origin in some remote ancestral form, it does not follow that they should now present close structural resemblances. It is far more important to show that they possess certain general features in common. The most important of their common features is undoubtedly their metameric origin. The nerve-supply forms another feature of fundamental importance, in which according to the interesting observations of Mr. Beard on "the segmental sense organs of the lateral line" (*Zool. Anz.*, VII, Nos. 161, 162) of the vertebrate, there is essential agreement. The developmental history of these lateral organs in the fish, where they make their first appearance as *segmental papillæ* in the strictest sense of these words, cannot at present be explained on a more satisfactory hypothesis.

¹ Dr. Eisig of the Naples Station is the original expounder of this view.

